VERTEBRATES FROM THE MIDDLE TRIASSIC OTTER SANDSTONE FORMATION OF DEVON

by A. R. MILNER, B. G. GARDINER, N. C. FRASER *and* M. A. TAYLOR

ABSTRACT. New vertebrate material from the Otter Sandstone Formation of Devon includes a cleithrolepidid fish, temnospondyl amphibians, a procolophonid reptile, and a tooth which may be attributed to a tanystropheid reptile. The Cleithrolepididae is represented by several specimens of *Dipteronotus cyphus*. The temnospondyl amphibian material includes two skull roof fragments referable to *Mastodonsaurus lavisi*, a skull and fragments assignable to the benthosuchid *Eocyclotosaurus* sp., and one mandibular fragment of an indeterminate large capitosaurid. The procolophonid material comprises several tooth-bearing fragments and a partial interclavicle, and appears to represent a relatively primitive form. A single tricuspid tooth most closely resembles those of the reptile *Tanystropheus*. An enigmatic elongate bone may be the neural spine of a *Ctenosauriscus*-like thecodontian or the rib of a dicynodont therapsid. No fish, capitosaurid, or procolophonid material has previously been described from the Otter Sandstone, and the benthosuchid *Eocyclotosaurus* has not previously been identified in the Triassic of the British Isles. Comparison of this vertebrate assemblage with those of Western and Central Europe and North America supports an Anisian age for the Otter Sandstone.

THE Otter Sandstone Formation is exposed along the south-east coast of Devon from Otterton Point near Budleigh Salterton to Port Royal, east of Sidmouth. It is a 118 metre thick Triassic sequence of largely fluviatile sandstones with included breccias and thin mudstone layers. It overlies the Budleigh Salterton Pebble Beds and is in turn overlain by 'marls' of the Mercia Mudstone Group. Warrington *et al.* (1980) and Laming (1982) reviewed the stratigraphy of the British Triassic and discussed the problems of correlating the Otter Sandstone with other Triassic sequences. The Otter Sandstone has proved difficult to date as it includes no volcanic rocks, and attempts to obtain spores have not been successful (Warrington 1971, and pers. comm. to M.A.T. 1984). The discontinuity at the base of the Budleigh Salterton Pebble Beds is usually taken as the base of the local Triassic, while palynomorphs have provided evidence for a Carnian (late Triassic) age for beds 135 m above the base of the Mercia Mudstone Group (Warrington 1971). The only evidence for a more precise dating of the Otter Sandstone Formation is the fossil vertebrates found within it.

In the nineteenth century, vertebrate material was collected from coastal exposures of the Otter Sandstone in two localities at least. Whitaker (1869) recovered a rhynchosaur specimen (GSM 90494) from a 'brecciated horizon' in the lower part of the Otter Sandstone Formation exposed in a low cliff on the west bank of the mouth of the River Otter. Later workers (Johnston-Lavis 1876; Metcalfe 1884; Carter 1888) found material of amphibians, reptiles, and coprolites (all BMNH) from fallen blocks ascribed to an 'ossiferous zone... ten feet from the top of the Sandstone' near High Peak, west of Sidmouth. Recently a large collection of vertebrate material (all EXEMS) has been made by Mr P. S. Spencer, principally from the north-eastern region of the exposure from Smallstones Point towards Sidmouth (Spencer and Isaac 1983, fig. 1) but also from a scattering of localities from Danger Point near the mouth of the Otter River eastwards to Port Royal at the mouth of the River Sid. Spencer and Isaac confirmed the early impression that the upper part of the Otter Sandstone is the most fossiliferous, specifying the top 20 m or so. A few specimens have been found *in situ*, but most have been recovered from fallen blocks and cannot be readily attributed to a specific horizon within the cliff section. Spencer and Isaac (1983) gave a preliminary account of the material which has now been subject to more detailed study. The rhynchosaur material has been described by Dr M. J. Benton (Bristol University) (Benton 1987, 1990), while much of the remaining new fish, amphibian and reptile material is described in the following account. Following the systematic description of this material, the age of the Otter Sandstone Formation is discussed.

Institutional abbreviations used in this work are: BMNH, British Museum (Natural History), London; EXEMS, Royal Albert Memorial Museum, Exeter, Devon; GSM, British Geological Survey, Keyworth, Nottinghamshire; NMI, National Museum of Ireland, Dublin; SMNS, Staatliches Museum für Naturkunde, Stuttgart; WARMS, Warwick County Museum, Warwickshire (WCM in earlier literature).

SYSTEMATIC PALAEONTOLOGY

Class OSTEICHTHYES
Subclass ACTINOPTERYGII
Infraclass ACTINOPTERI
Superdivision NEOPTERYGII
Plesion PERLEIDIFORMES
Family CLEITHROLEPIDIDAE Wade, 1935
Genus DIPTERONOTUS Egerton, 1854

Type species. *Dipteronotus cyphus* Egerton, 1854

Emended diagnosis. Deep-bodied fish in which the dorsal side is marked with a hump. Scaling characteristic, with fewer scales below lateral line than above it, and with extremely enlarged and pointed dorsal ridge scales between skull and dorsal fin. Head much deepened posteriorly, frontals greatly enlarged, and suspensorium upright. Orbit large, and two supraorbitals. Preoperculum vertical with a prominent pit-line ventrally and an infraorbital process which extends behind the triangular maxillary. Body lobe of tail reduced, rays 12–16 with expanded bases.

Remarks. Prominent dorsal ridge scales midway between the skull and dorsal fin are confined to *Pseudobeaconia* and *Dipteronotus* among cleithrolepidids. In *D. cyphus* they were originally mistaken for the bases of fin-rays (Egerton 1854, p. 369). Two further species of *Dipteronotus* have subsequently been described, namely: *D. aculeatus* from the Upper Buntsandstein (Scythian-Anisian) of France and Germany (Jörg 1969; Gall *et al*. 1974) and *D. gibbosus* from the Upper Triassic of Morocco (Martin 1980). These two species appear to be immediately related and together they form the sister-taxon to *D. cyphus* (Gardiner 1988).

Dipteronotus cyphus Egerton, 1854

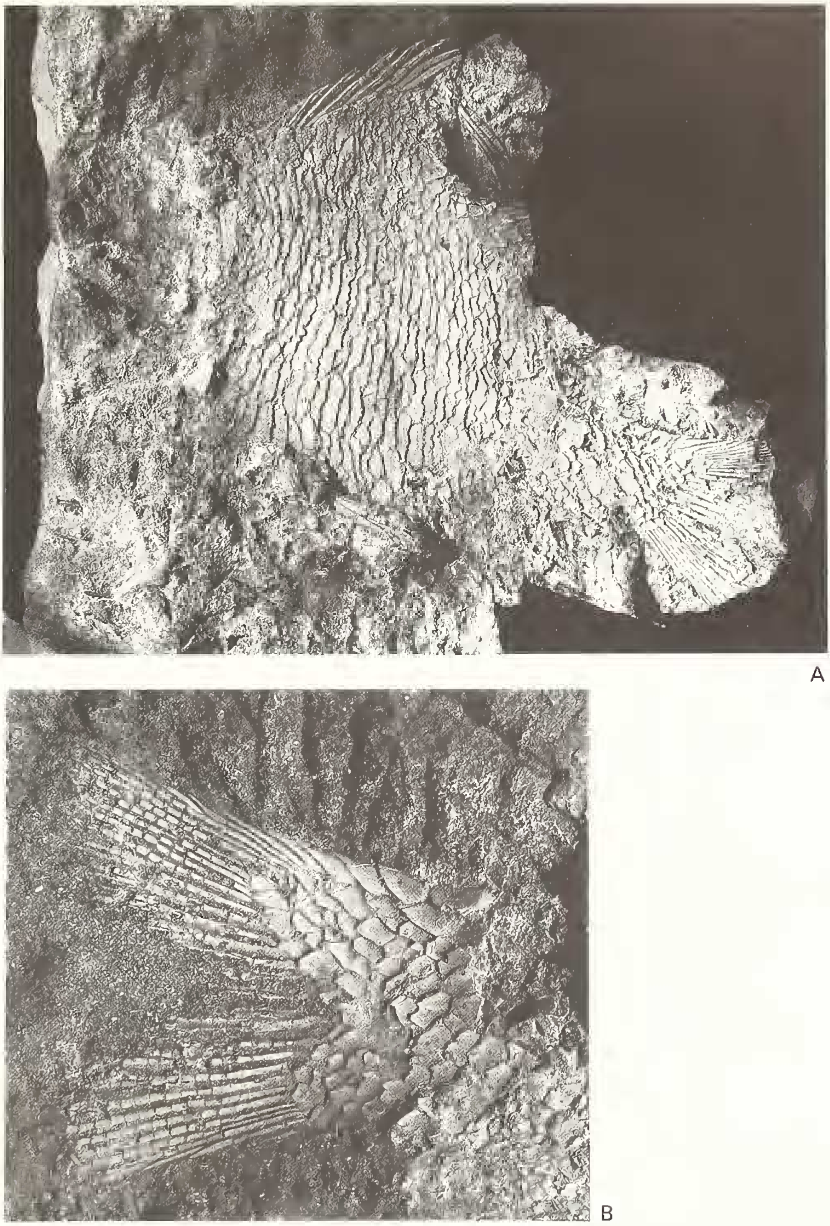
Text-fig. 1

1854 *Dipteronotus cyphus* Egerton, p. 369, pl. 11, figs 1 and 2.
1910 *Dipteronotus cyphus* Egerton; Woodward, p. 322.
1973 *Dipteronotus cyphus* Egerton; Hutchinson, p. 321.
1974 *Dipteronotus cyphus* Egerton; Gall *et al*., pp. 7–8, pl. 5.

Holotype. GSM 18188 and 18189, counterparts of an almost complete specimen, from the Bromsgrove Sandstone Formation, Middle Triassic of Bromsgrove, Hereford and Worcester (previously Worcestershire).

Referred material. NMI F.15677, a small fragment of body from the type locality. EXEMS 60/1985.293 and 294, two partial specimens in a fine mudstone from the Otter Sandstone Formation (Text-fig. 1). These specimens are better preserved than the holotype and have permitted a more accurate count to be made of the various fin-rays as well as a more detailed description of the scale ornamentation. Further specimens were collected and are in the EXEMS collection.

Emended diagnosis (based on holotype and EXEMS 60/1985.293 and 294). A *Dipteronotus* with



A

B

TEXT-FIG. 1. *Dipteronotus cyphus* Egerton. A, EXEMS 60/1985.293, entire specimen, ×1·5. B, EXEMS 60/1985.294, detail showing caudal fin, ×3.

10–13 elongate, spinose, ridge scales in front of dorsal fin; ventral ridge scales similar, but smaller than dorsals. Dorsal fin comprising 17 rays and 5 basal fulcra, and anal fin with about 14 rays and 2 fulcra. Tail with 27–30 rays of which the most dorsal 12 are epaxial and with three prominent basal fulcra dorsally and ventrally; pelvic fin with 5–6 rays. Dermosphenotic tall and narrow, and 2 infraorbitals. A single suborbital probably present between top of preoperculum and dermo-sphenotic. Scales with posterior crimping, those on dorsal hump having several rows of backwardly-pointing tubercles. On rest of body, scales are pectinate posteriorly with some ten projections.

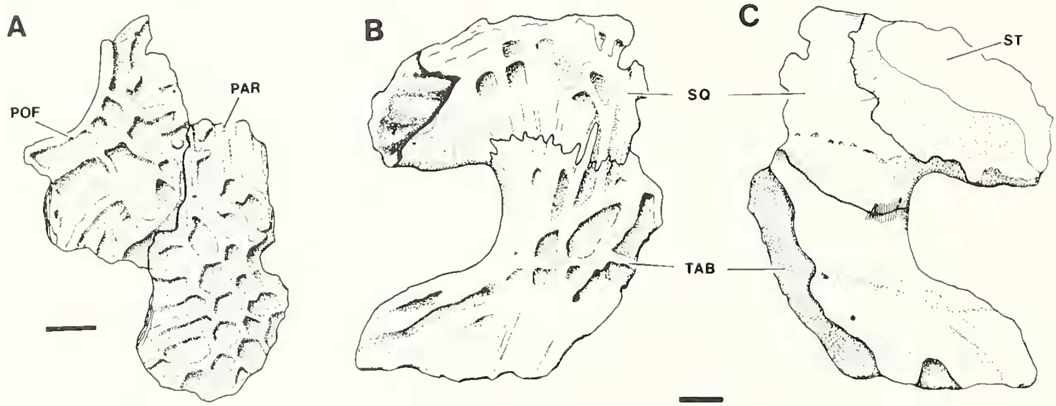
Class AMPHIBIA
Order TEMNOSPONDYLI
Family MASTODONSAURIDAE Lydekker, 1885
Genus MASTODONSAURUS Jaeger, 1828

Type species. *Salamandroides giganteus* Jaeger, 1828

Mastodonsaurus lavisi (Seeley) Paton, 1974 *nomen dubium*

Text-fig. 2A–C

1876 *Labyrinthodon lavisi* Seeley, p. 278, pl. 19, figs 1–3.
1916 *Labyrinthodon lavisi* Seeley; Wills, p. 15.
1947 '*Labyrinthodon*' *lavisi* Seeley; Romer, p. 228.
1962 '*Labyrinthodon*' *lavisi* Seeley; Watson, p. 252.
1965 *Labyrinthodon lavisi* Seeley; Welles and Cosgriff, p. 35 as a *nomen vanum*.
1974 *Mastodonsaurus lavisi* (Seeley); Paton, p. 282, figs 14B and 16B.



TEXT-FIG. 2. *Mastodonsaurus lavisi* (Seeley). A, EXEMS 60/1985.287, left postfrontal and parietal. B, C, EXEMS 60/1985.309, left tabular, squamosal and part of supratemporal in (B) dorsal and (C) ventral view. Abbreviations for Text-figs 2–4: FR, frontal; L, lacrimal; J, jugal; PAR, parietal; PO, postorbital; POF, postfrontal; PP, postparietal; PRF, prefrontal; QJ, quadratojugal; SQ, squamosal; ST, supratemporal; TAB, tabular. Scale bars, 10 mm.

Holotype. BMNH R.4215, posterior region of right mandible, collected by H. J. Johnston-Lavis from the Otter Sandstone Formation below High Peak, west of Sidmouth, Devon (Johnston-Lavis, 1876). Most recently figured by Paton (1974, figs 14B and 16B).

Remarks. Up to 1974, the specific name *lavisi* was restricted to a mandibular fragment from the Otter Sandstone. Paton (1974) revised the British Triassic temnospondyl material and combined the Midlands and Devon mastodonsaurid specimens as one species for which the senior specific name was *lavisi* borne by this specimen. The following description is restricted to Otter Sandstone specimens and unity of the Midlands material with *M. lavisi* is not assumed, although some comparison is made with specimens from Warwickshire.

Diagnosis. No species-level diagnosis can be given for the Otter Sandstone *Mastodonsaurus*. Paton's

(1974) diagnosis of *M. lavisi* is based on *Mastodonsaurus* generic characters which permit it to be distinguished only from contemporaneous capitosaurid material. Pending a revision of the species-level taxonomy of the German *Mastodonsaurus* material, there is no basis for diagnosing *M. lavisi*, but neither can it be assumed to be indeterminable. It seems most practical to retain the name, albeit as a *nomen dubium*, as a convenient label for the Otter Sandstone mastodonsaurid material.

Referred material from the Otter Sandstone. As *Mastodonsaurus lavisi* is a *nomen dubium*, the following *Mastodonsaurus* material is referred to that species solely on the basis of locality and horizon: BMNH R.331, posterior region of right mandible collected by H. J. Carter from the type locality (Carter 1888); four boxes of fragments collected by Carter are registered as R.331, but the mastodonsaur mandible is the only significant specimen; referred to *M. lavisi* by Paton (1974); EXEMS 60/1985.287, left postfrontal and parietal (Text-fig. 2A), collected by P. S. Spencer; EXEMS 60/1985.309, left tabular and parts of squamosal and supratemporal (Text-fig. 2B, C), collected by P. S. Spencer, and referred to by Spencer and Isaac (1983) as a fragment of *Cyclotosaurus*.

Description of new material. EXEMS 60/1985.287 (Text-fig. 2A) comprises the attached left postfrontal and left parietal of a large temnospondyl. Scaling these bones against a skull of *Mastodonsaurus cappelensis* figured by Wepfer (1923) suggests a midline skull length of 290 mm. The two bones bear coarse shallow sculpture with narrow ridge-systems. Some of the confluent sculpture pits on the orbital margin of the postfrontal may represent a lateral-line sulcus. The anterior end of the postfrontal is incomplete and it is impossible to ascertain whether it contacted the prefrontal or not. The postfrontal is relatively elongate and is almost as large as the parietal. The pineal foramen is situated about halfway along the parietals and hence well behind the posterior edge of the orbits.

The dermal sculpture resembles that of mastodonsaurids rather than capitosaurids and the large elongate postfrontal resembles that of the early mastodonsaurid *Mastodonsaurus cappelensis* from the Anisian of Kappel near Villingen, Baden-Württemberg, West Germany. Using WARMS Gz.20, a larger skull fragment of the Warwickshire *Mastodonsaurus* material, Paton (1974, table 1) was able to show that it also corresponded to *M. cappelensis* in orbit shape, size and position. In capitosaurids, the orbit length was 45–85% of the interorbital width, in WARMS Gz.20 and *M. cappelensis* 120–125%, in the larger Ladinian *Mastodonsaurus* species over 200%. Unfortunately, no comparative study has been undertaken of the various *Mastodonsaurus* specimens from the Anisian, Ladinian and Carnian of Baden-Württemberg and we do not know whether proportional differences such as those described above are of systematic significance or simply related to absolute size.

EXEMS 60/1985.309 (Text-fig. 2B, C) comprises the left tabular and parts of the squamosal and supratemporal of a very large temnospondyl. Scaled against figures of *Mastodonsaurus* skulls, it appears to be derived from a skull of about 600 mm midline length. The suture between the tabular and the other bones is densely convoluted. The sculpture on the dorsal surface of the bones is coarse and shallow. The tabular is a curved, slightly elongate bone thinning out at its distal extremity and clearly does not suture with any other bone behind the otic notch. The curvature of the tabular is such that the distal end was laterally rather than postero-laterally directed. The deep open otic notch, partly bordered by a long curved tabular bearing coarse sculpture, is characteristic of large specimens of *Mastodonsaurus*, but not of any particular species. Some specimens of *M. giganteus* from Gaildorf (e.g. SMNS 4707 and 54679) are very similar and the specimen is closely comparable to WARMS Gz.9 from Warwickshire (Paton 1974, fig. 6) which Paton attributed to *M. lavisi*. The new undescribed *Mastodonsaurus* material from the Lettenkeuper of Kupferzell (Wild 1980*b*) includes skulls over a wide size range which demonstrate that the tabular is small in skulls of 300 mm length but elongates later in ontogeny (A.R.M. pers. obs.). A few capitosaurids have similar tabulars (e.g. *Parotosuchus nasutus* Welles and Cosgriff 1965, fig. 19 and *Parotosuchus megarhinus* Chernin 1974, fig. 8) but the dermal sculpture is finer, deeper and more reticulate.

Discussion. The Mastodonsauridae is at present a neglected family. The full range of German *Mastodonsaurus* material has not been subjected to comprehensive comparative study this century and meaningful comparisons are still difficult. Beyond the genus *Mastodonsaurus*, there is uncertainty as to what constitutes a primitive mastodonsaurid. Some capitosauroids may in fact be primitive mastodonsaurids with only one or two of the specializations of *Mastodonsaurus*. *Kestrosaurus dreyeri* Haughton, 1925 has generally been considered to be an aberrant capitosaurid, but Ochev (1966) placed it in the new family Bukobajidae which Shishkin (1980) later reduced in synonymy with the Mastodonsauridae. '*Parotosaurus' lapparenti* Lehman, 1971 was also assigned to the Mastodonsauridae by Shishkin (1980). Both of these forms have double anterior palatal vacuities and laterally directed tabulars, and appear to be primitive mastodonsaurids with a gradistic resemblance to *Benthosuchus*.

The following observations can be made, however. Firstly, no mastodonsaurid-producing locality is known to have more than one species present. As the holotype of *M. lavisi* is a mandible from the Otter Sandstone, other mastodonsaur fragments from this formation can be placed under the name *M. lavisi* with confidence. Secondly, the proportions of the orbits and the circumorbital bones of specimens EXEMS 60/1985.287 from Devon and WARMS Gz.20 from Warwickshire both show the closest resemblance to the primitive *Mastodonsaurus cappelensis* Wepfer, 1923 from the Upper Bunter of Kappel in Baden-Württemberg, West Germany. This does not demonstrate the unity of the British material from the two areas not does it demonstrate synonymy with the German species. It suggests either that all three populations belong to a similar primitive evolutionary grade within the genus *Mastodonsaurus* or alternatively that all three populations are simply of similar-size specimens with similar orbital proportions. Because of the latter possibility, it is best to maintain the Warwickshire material as *Mastodonsaurus* sp. indet. (as no species name uniquely applies to it), the Devon material as *M. lavisi*, and the Kappel material as *M. cappelensis*, but the three populations may represent from one to three species of mastodonsaurid. Consequently, stratigraphical conclusions based on such material should be treated with great circumspection.

Family BENTHOSUCHIDAE Efremov, 1940
Genus EOCYCLOTOSAURUS Ortlam, 1970

Type species. *Eocyclotosaurus woschmidti* Ortlam, 1970

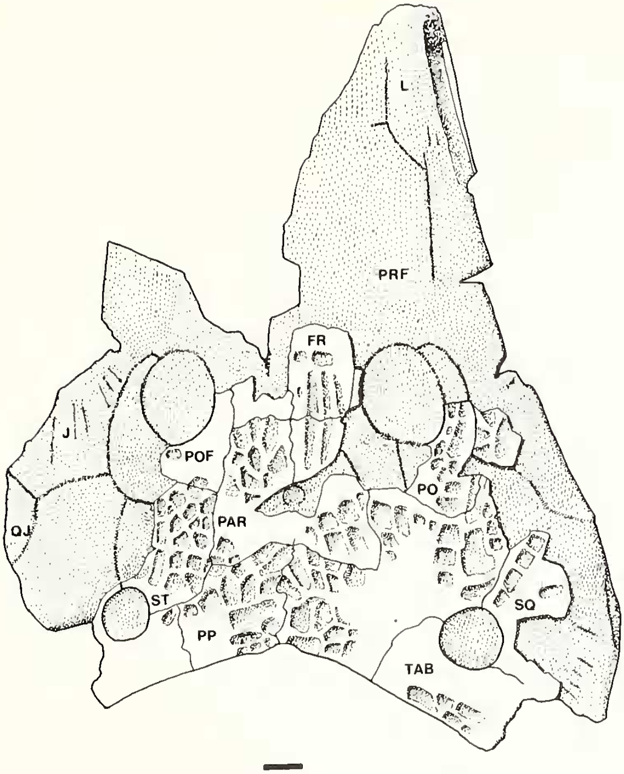
Eocyclotosaurus sp.

Text-figs 3 and 4.

Material. EXEMS 60/1985.72, damaged posterior skull roof with internal cast of left cheek (Text-fig. 3), from the Otter Sandstone below High Peak near Sidmouth, Devon and reported by Spencer and Isaac (1983) as a skull of *Cyclotosaurus*; EXEMS 60/1985.310, right tabular and parts of squamosal, supratemporal and postorbital (Text-fig. 4A); EXEMS 60/1985.75, an incomplete left clavicle (Text-fig. 4B), referred here with doubt; all collected by P. S. Spencer.

Description. EXEMS 60/1985.72 (Text-fig. 3), the most complete amphibian specimen yet collected from the Otter Sandstone Formation, is a partial skull of a small capitosauroid temnospondyl. Regions represented by bone include the skull table and parts of the interorbital area and cheeks; the rest of the cheeks and the right posterior region of the snout are represented by a weathered endocast, the part exposed at the time of collection. Most of the snout had already been weathered away prior to collection. The dermal bones of the right cheek, skull roof and interorbital region were all present *in situ* but were unfortunately damaged during excavation and have been reassembled. The palate is not exposed. The skull is estimated to have been 250 mm long, 150 mm wide from quadrate to quadrate, and 30 mm deep at the back, hence very low in profile. In most respects it is a typical capitosauroid skull and only key features need be discussed.

The dermal bones bear deep reticulate sculpture. There are no well-preserved lateral-line sulci although elongate pits on the supratemporals may represent poorly expressed sulci. The otic notch is completely closed by a stout extension of the tabular suturing with the squamosal. The length of this suture is about equal to the diameter of the otic notch. The posterior edge of the skull table is concave but appears to consist of two straight edges meeting medially at a distinct obtuse angle. The distal margin to the orbit is represented only by endocast on both sides, but on the left side the suture-lines are clearly visible. They show that the jugal was excluded from the orbit margin by an anterior extension of the postorbital extending forwards to the anterior margin of the orbit. Although the prefrontal shape is not determinable, it is probable that the postorbital sutured with the prefrontal ahead of the orbit; the postorbital has the same anterior extent as in German and French *Eocyclotosaurus* specimens in which suturing with the prefrontal occurs. Part of the corresponding suture is

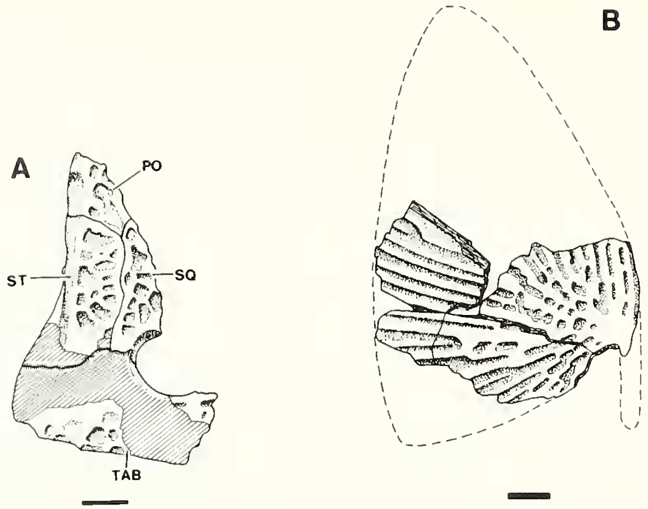


TEXT-FIG. 3. *Eocyclotosaurus* sp. EXEMS 60/1985.72, incomplete skull roof in dorsal view. Abbreviations: see Text-figure 2. Scale bar, 10 mm.

visible on the endocast on the right side as well (Text-fig. 3). The relationship between the prefrontal, the postfrontal and the frontal is unfortunately difficult to observe because of damage to the bones. On the right side, the pre- and postfrontals are represented only by damaged scraps of bone but the frontal appears to be inset with an exposed sutural edge along its distal margin. This indicates that the pre- and postfrontals probably met mesially to the orbit and excluded the frontal from the orbit margin. Although the snout is poorly preserved, it can be seen that the sides converge anteriorly, which implies a narrow anterior snout, rather than a broad parallel-sided snout.

Discussion. The specimen is clearly one of the capitosaurid or benthosuchid temnospondyls with a completely enclosed otic notch. In the Triassic of western Europe, the genera *Cyclotosaurus*, *Stenotosaurus*, and *Eocyclotosaurus* all have such notches. Their characteristics and relationships have recently been discussed by Kamphausen and Morales (1981), Kamphausen (1983) and Morales and Kamphausen (1984). The apparently narrowing snout and the anteriorly extending postorbital excluding the jugal from the orbit margin characterize the genera *Eocyclotosaurus* and *Stenotosaurus*. *Cyclotosaurus* species have the jugal entering the orbit margin and have broad snouts. The prefrontal-postfrontal contact identifies the specimen as *Eocyclotosaurus* rather than *Stenotosaurus* in which the frontal enters the orbit margin. These character-states suggest that the specimen is a skull of *Eocyclotosaurus* and all other visible features are consistent with this identity.

Kamphausen and Morales (1981) established the generic unity of the *Eocyclotosaurus* material from the Upper Bunter of France and West Germany but did not attempt to provide separate diagnoses for the two species *E. lehmani* (Heyler) and *E. woschmidti* Ortlam. There are no obvious discriminating features between the species as described and the problem of whether this material



TEXT-FIG. 4. *Eocyclotosaurus* sp. A, EXEMS 60/1985.310, fragment of right skull table. B, EXEMS 60/1985.75, incomplete left clavicle. Abbreviations: see Text-figure 2. Scale bar, 10 mm.

represents one or two species is still being studied by Kamphausen. For this reason, the Otter Sandstone material is not assigned to a species but simply identified as *Eocyclotosaurus* sp.

Possible further referred material. The following two specimens are not in themselves diagnostic but are consistent with attribution to *Eocyclotosaurus* sp. and can be referred here with various degrees of confidence.

EXEMS 60/1985.310 (Text-fig. 4A) is a fragment of dermal skull roof from the region of the right otic notch. It is made up of an abraded right tabular and well-preserved parts of the right supratemporal, squamosal, and postorbital. The sculpture is relatively deep and reticulate. The supratemporal has broken along the lateral-line sulcus and only the distal part of the bone remains. The sulcus can be seen to be deep but its width cannot be determined. The otic notch is closed, the tabular running behind it as a stout structure, broadening distally towards the region where it would meet the squamosal. The specimen appears to be identical in all significant respects with the corresponding region in EXEMS 60/1985.72 and may also be referred to *Eocyclotosaurus* sp.

EXEMS 60/1985.75 (Text-fig. 4B) is an incomplete left clavicle of a capitosauroid temnospondyl. In shape, size, and texture of sculpture it is most consistent with attribution to the cranial material described above and is cautiously referred here.

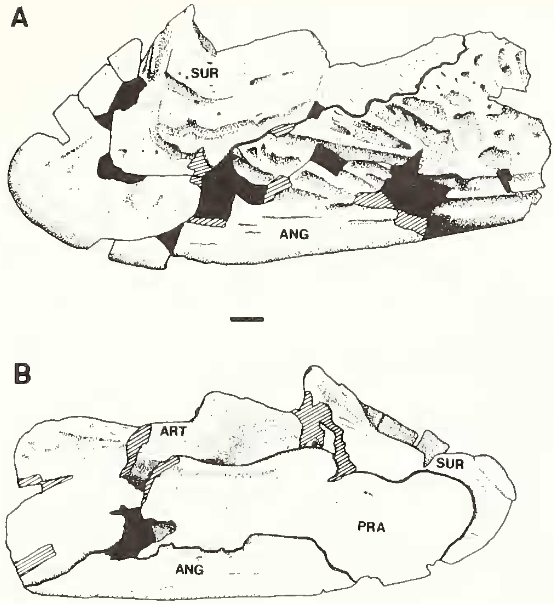
Family CAPITOSAURIDAE Watson, 1919
Capitosauridae *incertae sedis*

Text-fig. 5

Material. EXEMS 60/1985.78, posterior region of right mandible (Text-fig. 5A, B), collected by P. S. Spencer, and referred to by Spencer and Isaac (1983) as a mandible of *Cyclotosaurus*.

Description. This specimen comprises the greater part of the post-dentary region of a massive right mandible. The preserved elements are the surangular, prearticular, articular, and the posterior region of the angular. The angular bears deep coarse sculpture which extends slightly on to the surangular. A broad, shallow lateral-line sulcus, the mandibular sulcus, extends back from the ventrodistal side of the angular and curving dorsally behind it up to the dorsal side of the retroarticular process (Text-fig. 5A). Two branches extend forward along the external face of the surangular, the lower is the oral sulcus and the upper is the accessory sulcus (terminology as in Jupp and Warren 1986). Behind the mandibular sulcus, the external face of the retroarticular process has a few striations but does not have a sculptured surface. The ventral edge of the mandible is narrow

TEXT-FIG. 5. Capitosauridae *incertae sedis*. EXEMS 60/1985.78, posterior region of right mandible. A, buccal view. B, lingual view. Abbreviations: ANG, angular; ART, articular; PRA, prearticular; SUR, surangular. Scale bar, 10 mm.



and sharply concave. The retroarticular process is broadly rounded in lateral aspect, and is a slightly elongated triangle in dorsal view. The articular surface with the quadrate is saddle shaped. The foramen for the chorda tympani is present and set high on the side of the jaw.

Discussion. Comparison with the mandibular fragments described and tabulated by Paton (1974, table 2) shows complete correspondence to the Warwickshire specimens which she assigned to *Cyclotosaurus pachygnathus*. The nature of the sculpture and the lateral-line sulci, the high position of the chorda tympani foramen, the absence of sculpture on the retroarticular process and the shape of that process all serve to identify it as a capitosaurid or benthosuchid rather than a mastodonsaurid. It is clearly not attributable to *M. lavisi*. The massive construction and the saddle-shaped articular surface correspond to those of a large *Cyclotosaurus* or *Parotosuchus* rather than a lightly built *Stenotosaurus* or a benthosuchid. It has all the characteristics of those Warwickshire mandibles such as GSM 27964 that Paton assigned to *Cyclotosaurus pachygnathus*. However, referring this specimen to *C. pachygnathus* is unsatisfactory because, by Paton's (1974, p. 280) own admission, *C. pachygnathus* is an undiagnosed aggregation of large cyclotosaur material from Warwickshire placed under one name for systematic stability and general convenience. Some of it certainly pertains to a *Stenotosaurus* or *Cyclotosaurus* of massive construction, but is of uncertain unity, cannot be comparatively diagnosed with the German material, and is effectively Capitosauridae *incertae sedis*, with the name *C. pachygnathus* a *nomen dubium* restricted to the lectotype specimen designated by Paton. However, much of the Warwick material is not demonstrably cyclotosaurian. In assuming the unity of this capitosaurid material, Paton did not attempt to compare any of it with open-notched *Parotosuchus* and *Eryosuchus*, both of which are present in Middle Triassic assemblages. A fragment of massive capitosaurid which does not include the otic notch is as likely to be *Parotosuchus* or *Eryosuchus* as *Cyclotosaurus*. Morales (1987) has noted that there is no certain *Cyclotosaurus* material from pre-Carnian beds and that '*Cyclotosaurus*' *randalli* Welles, 1947 from the Middle Triassic of the Moenkopi Formation is indeterminate but probably a benthosuchid. As the Otter Sandstone specimen is from a geographically distinct locality, and as unwarranted stratigraphical assumptions might be drawn if it and the Warwickshire material were assigned to the same genus or species, it is simply assigned to Capitosauridae *incertae sedis*.

Indeterminate temnospondyl fragments

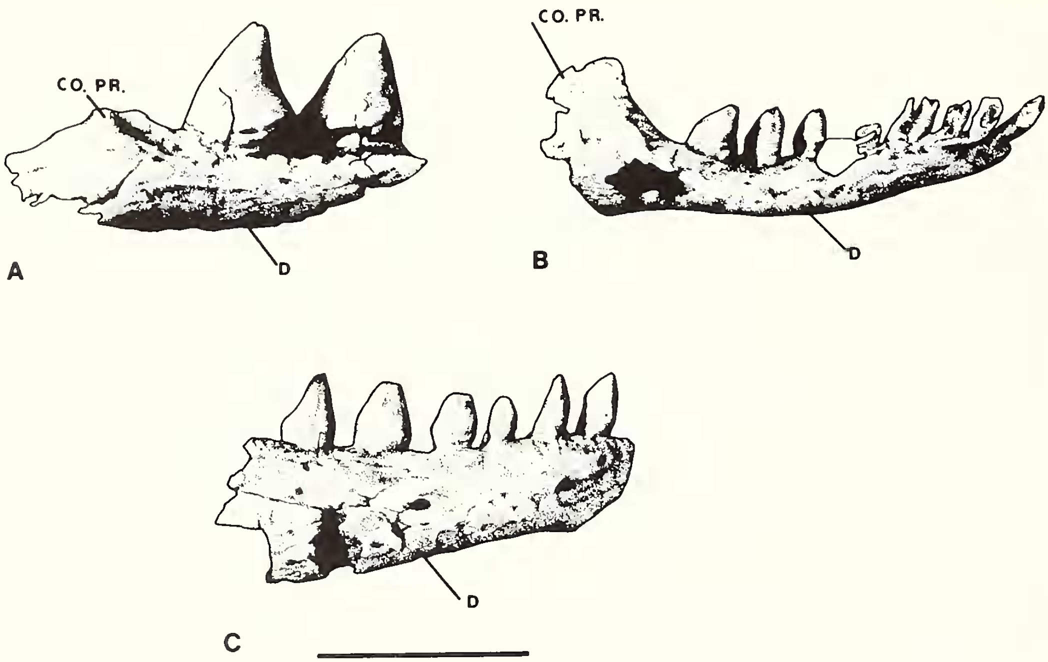
Several other specimens from the Otter Sandstone clearly derive from temnospondyl amphibians but are not determinable. Six of these specimens which have numbers prefixed by EXEMS 60/1985, are as follows: .4, .79, .183, labyrinthodont teeth or palatal tusks; .96, .148, fragments of sculptured dermal bone, probably from skull roof; .308, half of a small interclavicle. A seventh specimen is EXEMS 7/1986.2, the posterior half of the right prefrontal of a benthosuchid or capitosaurid.

Class REPTILIA
Order PROCOLOPHONIA
Family PROCOLOPHONIDAE Cope, 1889

Procolophonidae *incertae sedis*

Text-figs 6 and 7A, B

Material. EXEMS 60/1985.87, a right dentary fragment (Text-fig. 6A), referred to by Spencer and Isaac (1983) as a specimen of the procolophonid *Leptopleuron*; EXEMS 60/1985.154, a right dentary (Text-fig. 6B), reported as a sphenodontid by Spencer and Isaac (1983); EXEMS 60/1985.311, an incomplete right dentary (Text-fig. 6C), EXEMS 60/1985.3, a fragmentary left maxillary (Text-fig. 7A), reported by Spencer and Isaac (1983) as a sphenodontid; EXEMS 60/1985.9, an incomplete interclavicle (Text-fig. 7B), correctly identified by Spencer and Isaac (1983). All specimens were collected by P. S. Spencer.

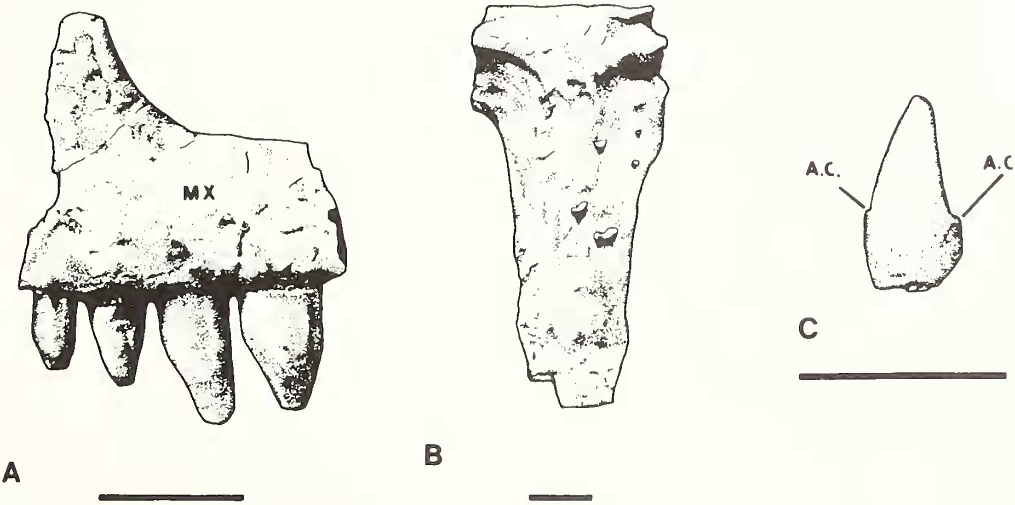


TEXT-FIG. 6. Procolophonidae *incertae sedis*. A, EXEMS 60/1985.87, fragment of right dentary. B, EXEMS 60/1985.154, juvenile right dentary. C, EXEMS 60/1985.311, juvenile right dentary. All in lateral view. Abbreviations: CO. PR., coronoid process; D, dentary. Scale bar, 5 mm.

Description. EXEMS 60/1985.87 was the only jaw specimen correctly identified by Spencer and Isaac (1983) as procolophonid, but whether it can be attributed to *Leptopleuron*, as they suggest, is questionable. The dentary, which is predominantly exposed in lateral aspect (Text-fig. 6A), is 9·0 mm long and, in addition to the two posteriormost teeth, it retains the broken base of a coronoid process. Superficially at least, the broadly-based obtusely conical teeth display an acrodont attachment. The posterior tooth is 2·7 mm high and that in front of it is 2·4 mm high. Their bulbous appearance in lateral aspect is typically procolophonid. The teeth of this specimen (the only one in which they are completely exposed from the matrix) are not transversely broadened. However the maximum development of transverse broadening in procolophonids is seen most frequently in the teeth immediately anterior to these positions.

Two further dentary fragments are more complete, but somewhat smaller than EXEMS 60/1985.87, and they are regarded here as juveniles. EXEMS 60/1985.154 is 12 mm long and retains nine teeth and a pronounced coronoid process (Text-fig. 6B). The element is complete anteriorly, with the mandibular symphysis partly embedded in matrix. Spencer and Isaac (1983, p. 268) referred to this specimen as a sphenodontid, but it lacks typical sphenodontid dental characters such as tooth flanges, distinct successional hatchling and additional tooth series, and at least partial alternation in tooth size (Fraser 1986*a*; Whiteside 1986), nor is there a marked posteriorward increase in tooth height, nor any indication of extensive lateral wear facets correlated with the shearing jaw action so typical of sphenodontids (Robinson 1973; Gorniak *et al.* 1982; Fraser and Walkden 1983). Where exposed, wear facets appear to be confined to the apical surfaces of each tooth. The prominent incisiform anterior teeth are inclined anteriorly and somewhat laterally, a characteristic readily observed in *Procolophon* and *Orenburgia*.

EXEMS 60/1985.311 (Text-fig. 6C) is a third dentary fragment, also exposed from the right side. It is incomplete posteriorly and lacks the coronoid process, but the six exposed teeth are rather better preserved than in the previously described specimens. In all specimens, tooth attachment appears to be acrodont. The first two teeth are equal in height to the more posterior members of the tooth row, yet they are markedly narrower and thus incisiform in appearance. By contrast, the posterior three teeth are broader based, and in lateral aspect they are widest at a point approximately mid-way up the crown. The resulting profile has been described as barrel-shaped by Malan (1963) and characterizes most procolophonids (e.g. *Procolophon*, *Thelegnathus*, *Tichvinskia*).



TEXT-FIG. 7. A and B, Procolophonidae *incertae sedis*; A, EXEMS 60/1985.3, left maxillary in lateral view; B, EXEMS 60/1985.9, interclavicle in ventral view. C, ?*Tanystropheus* sp., EXEMS 60/1985.143, an isolated tooth. Abbreviations: A.C., accessory cusps; MX, maxillary. Scale bar, 2 mm.

EXEMS 60/1985.3 is a maxillary fragment bearing four teeth (Text-fig. 7A) which Spencer and Isaac (1983) referred to as a sphenodontid. They believed it to represent a right element in association with a partly preserved jugal. Presumably they took a faint line running across the specimen as the suture between the two bones. However the dental morphology is consistent with that of a procolophonid and, other than the acrodont implantation, the dentition shows no sphenodontid characteristics. The enlarged orbit of procolophonids is characterized by the great expansion of the posterodorsal corner so that the ventral margin, normally formed by the jugal and (to a variable extent) the maxillary, gently slopes posterodorsally. The preserved orbital margin of EXEMS 60/1985.3 is too abrupt for it to be anything but the anterior margin. Furthermore the slight recurvature of the teeth supports the interpretation of this fragment as part of a left-sided element. Consequently, if the line referred to above is a suture, then it is between the lacrimal and maxillary rather than the jugal and maxillary. However the line is poorly defined and it seems more plausible to attribute it to post-mortem damage.

EXEMS 60/1985.9 is an incomplete T-shaped interclavicle (Text-fig. 7B) which is characteristically procolophonid. Although the interclavicles of sphenodontids are also T-shaped, they are usually much more slender and they lack the broad median bar that is so prominent in EXEMS 60/1985.9.

Discussion. There is nothing to suggest that more than one procolophonid species is represented in the Otter Sandstone, and the variation in size can be satisfactorily explained as ontogenetic. The only characteristics which may be of systematic or stratigraphical value are those of the mandibular dentition, which may be summarized as follows: the mandible possesses nine acrodont teeth (a primitively high number within the Procolophonidae), the anterior incisiform teeth are inclined anterolaterally, and the posterior molariform teeth are barrel-shaped (procolophonid characters) but appear to lack the derived conditions of being cuspidate or transversely broadened. The Otter Sandstone material thus appears to belong to a primitive procolophonid and its closest resemblance is to the Middle Triassic (Anisian) *Anisodontosaurus greeri* from the Holbrook Member of the Moenkopi Formation of Northern Arizona. Although *Anisodontosaurus* was recorded by Welles (1947) as Reptilia *incertae sedis*, and by Murry (1987) as a primitive sphenodontid, it appears to be a primitive procolophonid. The dentary bears twelve teeth differentiated into incisiforms and broad-based molariforms. Welles (1947) described the two posteriormost teeth of *Anisodontosaurus* as acrodont in implantation, but noted that the more anterior teeth project further down into the dentary and approach a thecodont condition. However, it is sometimes impossible clearly to distinguish between different forms of tooth implantation (Fraser and Shelton 1988). Although procolophonids are normally considered to be acrodont, the teeth in some specimens appear to be positioned in shallow sockets (Fraser 1986*b*), not unlike the tooth implantation described in *Anisodontosaurus*. Although the former possesses rather more teeth, *Anisodontosaurus* and the Otter Sandstone procolophonid are primitively more similar to each other than to any other procolophonid.

Typical early Triassic procolophonids such as *Procolophon*, *Koiloskiosaurus*, *Sclerosaurus*, *Eumetabolodon*, and *Thelegnathus* are more derived than the Otter Sandstone form in that they have transversely broadened 'molariform' teeth, and a rudimentary bicuspidate condition is sometimes present. The dentitions of *Koiloskiosaurus* and *Sclerosaurus* from the Upper Buntsandstein of Germany are incomplete but, although they appear to possess between seven and nine teeth in each jaw ramus, at least some of these are transversely broadened (Huene 1911, 1943). In late Triassic forms, the bulbous profile is accentuated and the molariform teeth are invariably transversely broadened and either bicuspidate (*Leptopleuron*) or tricuspidate (forms in the English fissure sediments (Fraser 1986*b*)).

Some early and most late Triassic procolophonids show a marked trend towards reduction in overall tooth numbers. The third Buntsandstein genus, *Anomoiodon* (Huene 1939), is small with a skull length just over 30 mm and hence close in size to the Otter Sandstone material. *Anomoiodon* resembles the Otter Sandstone material in that all the marginal teeth are conical and no transverse broadening is apparent. On the other hand, despite the incomplete preservation, there would appear to have been no more than five teeth in the mandible in contrast to nine in EXEMS 60/1985.54. Thus there is no clear basis for assigning the Devon specimens to any one of the contemporaneous German genera. The Otter Sandstone procolophonid material is too fragmentary to be determinable below family level, but it does appear to belong to a very primitive number of the family.

Division ARCHOSAUROMORPHA
Order PROLACERTIFORMES
Family TANYSTROPHEIDAE Romer, 1945
Genus TANYSTROPHEUS Meyer, 1852

cf. *Tanystropheus* sp.

Text-fig. 7C.

Material. EXEMS 60/1985.143, a tricuspid tooth (Text-fig. 7C), collected by P. S. Spencer, and reported as a therapsid tooth by Spencer and Isaac (1983).

Description. A single tricuspid tooth, approximately 1·0 mm high, bearing two small accessory cuspules on either side of the main cusp. There is some resemblance to the large teeth of the Norian pterosaur *Eudimorphodon* (Wild 1978), but the latter are considerably larger and more elongate. A better comparison is with the teeth of the prolacertiform *Tanystropheus* (Wild 1973, 1980*a*). Wild (1980*a*, fig. 4) figures several teeth from a *Tanystropheus* skull including the fourth dentary tooth (fig. 4*c*) which is almost identical to 60/1985.143 in overall shape and relative size of cusp and cuspules.

Class AMNIOTA *incertae sedis*

Material. EXEMS 60/1985.88, an elongate bone collected by P. S. Spencer. Referred to by Spencer and Isaac (1983, p. 269) as a neural spine of 'the pelycosaur *Ctenosaurus*'.

Description. This specimen is a long straight bone, 514·9 mm in length according to Spencer and Isaac, but broken at both ends. It has a slightly flattened figure-of-eight cross-section and a surface pattern of fine ridges and foramina. It seems to be part of the axial skeleton of a large reptile, but beyond this general identification, it has proved difficult to place anatomically or systematically. As well as two of the authors (A.R.M. and M.A.T.), several colleagues, including Drs M. J. Benton, A. R. I. Cruickshank, G. M. King, and D. B. Norman have examined the specimen. There is no basis for attributing it to the pelycosaurs, and in fact the Triassic '*Ctenosaurus*' material, now renamed *Ctenosauriscus*, has been shown by Krebs (1969) to be one of a series of long-spined Middle Triassic thecodontian-grade archosaurs. In the specimen from the late Middle Buntsandstein figured by Krebs (1969, pl. 1), the tallest neural spine is a long straight flattened bone about 640 mm long. The Otter Sandstone specimen could be a long neural spine of such a ctenosauriscid or a rib of a large dicynodont therapsid such as a kannemeyeriid. Its size is compatible with either identity but it appears to be somewhat narrow in relation to its length for either interpretation. There is slight asymmetric curvature at one end which seems to be too great for a ctenosauriscid spine and too little for a dicynodont rib. The identity of this specimen is left open.

STRATIGRAPHY

Recent history

As noted in the introduction, the only available evidence for dating the Otter Sandstone is the vertebrate fossil fauna itself. Previously, only the few fragments of rhynchosaur and temnospondyl collected in the nineteenth century have been considered for the purposes of dating. Walker (1969) noted the Sidmouth rhynchosaur as 'a more primitive species' of *Rhynchosaurus* than those known from the Midlands and Shropshire. The Midlands *Rhynchosaurus* derives from the Bromsgrove Sandstone Formation of the Sherwood Sandstone Group, while the Shropshire material derives from the Helsby Sandstone Formation of the Sherwood Sandstone Group and the Tarporley Siltstone Formation of the Mercia Mudstone Group (Warrington *et al.* 1980). However, no precise independent dating of the Midlands or Shropshire reptiles had then been achieved and Walker could only suggest an age within the range of late Anisian to earliest Carnian, probably early-mid Ladinian. Unfortunately, Walker (1969) did not explicitly state whether this dating also applied to the Otter Sandstone material. As a result, Laming (1982) cited Walker as ascribing an early-mid Ladinian age to the Devon rhynchosaur, whereas Warrington *et al.* (1980) and Spencer and Isaac (1983) took Walker's statement that the Devon rhynchosaur was more primitive to imply an Anisian date for the Otter Sandstone Formation. Walker later (1970) said of the Shropshire and Midlands animals that 'a late Anisian, or, preferably, a Ladinian age seems to be implied'. He also repeated his opinion that the Devon material was more primitive and tentatively suggested that the

Otter Sandstone Formation was older than the Shropshire and Midlands horizons, and so presumably an Anisian age was implied. Most subsequent assignments of an Anisian date to the Otter Sandstone Formation can be traced back to Walker's observation (see Benton 1990 for a discussion). The English *Rhynchosaurus* material, including several new specimens from the Otter Sandstone, has recently been restudied by Benton (1987, 1990). The Otter Sandstone *Rhynchosaurus* represents a distinct species from the Midlands material but the characters of the various species do not suggest any obvious stratigraphical sequence of the British Triassic sites (Benton 1990).

Paton (1974) reviewed the temnospondyl amphibians of the English Triassic and suggested that the Otter Sandstone vertebrates were coeval with the Shropshire and Midlands animals. She associated Devon and Midlands *Mastodonsaurus* material in the single species *M. lavisi* which implied that the two horizons were contemporaneous. Paton compared the mastodonsaur and the two cyclotosaur species from the English Triassic with German material and argued that *M. lavisi* and *Cyclotosaurus leptognathus* indicated a Scythian/Anisian age, while *Cyclotosaurus pachygnathus* indicated a Carnian/Norian age. She appears to have taken an average of the two ages, ascribing the Midlands and Devon amphibians to the early Ladinian, after taking Walker's (1969, 1970) reptile evidence into account. Thus the previously published situation for the age of the Otter Sandstone Formation vertebrates is that it is either Anisian (based on Walker's suggestion that the rhynchosaur is more primitive than the presumed Ladinian Midlands material) or Ladinian (based on Paton's conclusion that the material is contemporaneous and that two of the amphibians suggest an Anisian age and one suggests a Carnian age).

New evidence

Attempts to date the British Triassic vertebrate-bearing assemblages by comparison with the French and German sequences are handicapped by the presence of the Muschelkalk through much of the Anisian and Ladinian in mainland Europe. Consequently, comparisons of continental vertebrates must either be with the Upper Buntsandstein/Röt/*Voltzia* Sandstone faunas of uppermost Scythian/basal Anisian age, or with the Lettenkohle faunas of latest Ladinian age. Middle Anisian-Middle Ladinian continental faunas are barely represented in the Muschelkalk, and there are no sequential series of stratigraphically restricted taxa, and so only relatively crude comparisons and correlations are possible. Of the new material reported in this work, the capitosaurid jaw is least useful, merely supporting a Triassic age for the Otter Sandstone. All other forms can be used to narrow the possibilities to give a more precise assessment.

The genus *Dipteronotus* is known from the Scythian of Europe to the Carnian/Norian of Morocco but the Otter Sandstone species *D. cyphus* is otherwise known only from the fish assemblage from the Building Stones, the upper member of the Bromsgrove Sandstone Formation at Bromsgrove. Warrington (1967, 1970) dated the entire Bromsgrove Sandstone in a borehole at Bromsgrove as Scythian to early Ladinian using acritarch and miospore evidence, and this would imply an Anisian – early Ladinian age for *D. cyphus*. Comparisons of Bromsgrove vertebrates with material from Germany suggest a date at the later end of this range, particularly the presence of the shark *Palaeobates keuperinus* (*Acrodus* sp. of Wills 1907, 1910) and the palaeoniscoid *Gyrolepis albertii* (see Appendix for further details). *Palaeobates keuperinus* (Murchison and Strickland) occurs at several localities in the Bromsgrove Sandstone Formation and the Mercia Mudstone Group (it may be noted that the material of *Phoebodus brodei* Woodward from Shrewley consists of symphysial teeth of *Palaeobates keuperinus*). *P. keuperinus* resembles closely *P. angustissimus* (Agassiz) from the Upper Muschelkalk and Lettenkohle of Germany, Poland, and France. *G. albertii* is not only found in the Bromsgrove Sandstone Formation and Mercia Mudstone Group of the Midlands, but also continues into the Rhaetic. This species also occurs in Baden-Württemberg, Bavaria, and Thuringia where it is almost entirely confined to the Upper Muschelkalk. Thus *Dipteronotus cyphus* at Bromsgrove is in a horizon of Anisian to early Ladinian age and is associated with some fish found in the Ladinian upwards elsewhere. A late Anisian – early Ladinian age might be inferred for the Otter Sandstone on the basis of the presence of *D. cyphus*.

The genus *Eocyclotosaurus* has the most restricted stratigraphical range of any form described here. *Eocyclotosaurus* species have been described from two European formations, *E. lehmani* from the *Voltzia* Sandstone of the Vosges in France and *E. woschmidti* from the Lower Röt of the Schwarzwald in West Germany. Both formations are equated with the Upper Bunter and are either late Spathian or early Anisian (uppermost Lower or lower Middle Triassic) in age (Morales 1987). There is also an undescribed eocyclotosaur, which is being studied by S. P. Welles and M. Morales (Morales 1987), from the Holbrook Member of the Moenkopi Formation of Arizona, which is believed to be early Anisian in age (Welles and Estes 1969; Morales 1987). The presence of this genus very positively suggests an Anisian age for the Otter Sandstone.

Mastodonsaurus species have been described from the Upper Bunter (Anisian) of Kappel in West Germany (*M. cappelensis*) to the Schilfsandstein (Carnian) of Feuerbacher Heide, Stuttgart (*M. keuperinus*). As discussed above, the British material from both Devon and Warwickshire has some resemblance in interorbital proportions to the Anisian *M. cappelensis* within the genus. However, in the absence of detailed comparisons among the Anisian, Ladinian, and Carnian *Mastodonsaurus* material from Germany, not much weight can be given to this observation and the material merely indicates an Anisian-Carnian date.

The procolophonid, though not precisely determinable, is clearly primitive in the number and narrowness of the mandibular teeth, and forms with such primitive features are found only in Scythian and Anisian horizons. Other reptiles clearly indicate a Middle Triassic age. The comparison of the isolated tricuspid tooth with the dentition of *Tanystropheus* supports a Middle Triassic assignment, *Tanystropheus* being known from the Anisian and the Ladinian of central Europe (Wild 1980*a*). If the elongate element proves to be a ctenosauriscid neural spine, this also supports a Middle Triassic age. Known ctenosauriscids are *Ctenosauriscus* from the Anisian Upper Buntsandstein of Germany (Krebs 1969), *Hypselorhachis* from the Ladinian Manda Formation of Tanzania, and *Lotosaurus* from the Middle Triassic of China.

A consideration of the Otter Sandstone assemblage as an association supports an Anisian age. The association of *Dipteronotus cyphus* (Anisian-basal Ladinian), *Eocyclotosaurus* (late Scythian-Anisian), *Mastodonsaurus* (Anisian-Carnian), primitive procolophonid (Scythian-Anisian), ?ctenosauriscid (Anisian-Ladinian) and ?tanystropheid (Anisian-Ladinian) has the Anisian as the only shared date. The fauna is in fact reminiscent of the Scythian/Anisian late Buntsandstein and *Voltzia* Sandstone faunas of Germany and France (Jörg 1969; Krebs 1969; Ortlam 1970; Gall *et al.* 1974; Kamphausen and Morales 1981), although *Rhynchosaurus* is conspicuously absent from the latter assemblages. The resemblance suggests that the Otter Sandstone fauna is an extension of the Anisian Upper Buntsandstein fauna.

THE OTTER SANDSTONE FAUNA

The Otter Sandstone appears to have been laid down on a flood-plain covered with small ephemeral braided streams and lakes (Laming 1982). The climate was semi-arid with long dry periods punctuated by seasonal rains and flash-floods. The vertebrate material is fragmentary, clearly transported and current-sorted, which can be inferred from the composition of the assemblage; teeth, tooth-bearing elements, and dense pieces of skull and pectoral girdle. The notable exception is the *Dipteronotus* material which is found as intact specimens in a laminated mudstone. Because of the derived nature of the assemblage, it bears an uncertain relationship to the original fauna (or faunas) and only a few observations can be made.

There seems to be distinct aquatic and terrestrial components to the fauna. The three types of temnospondyl amphibian were all superficially crocodile-like forms and all belong to families which are believed to have been fundamentally aquatic. The presence of three types of aquatic carnivore, some growing to at least 2 metres in length, suggests a rich fish fauna of which we currently have only one genus. It also suggests that there must have been at least some permanent water bodies among the aquatic environments on the flood-plain which gave rise to the Otter Sandstone.

The only frequent elements in the terrestrial fauna are the rhynchosaur *Rhynchosaurus*, a medium-sized herbivore, and the procolophonid, a small herbivore. Both appear to have been adapted for feeding on particularly durable vegetation. The long bone appears to have represented a rarer medium-large herbivore, whether it belonged to a ctenosauriscid or a dicynodont. Notwithstanding earlier reports, there are no sphenodontids or insectivorous/carnivorous therapsids in the collected material. Spencer and Isaac (1983, p. 269) noted teeth and a skull fragment of an *Ornithosuchus*-like medium-sized carnivore. At present, the terrestrial component of the Otter Sandstone fauna does not appear to be diverse and perhaps consists of representatives of a few abundant specialists living in a semi-arid flood-plain environment.

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A. R. MILNER
Department of Biology
Birkbeck College
Malet Street
London WC1E 7HX

B. G. GARDINER

Department of Biology
Kings College London
Campden Hill Road
London W8 7AH

N. C. FRASER

Virginia Museum of Natural History
1001 Douglas Avenue
Martinsville
Virginia 24112, USA.

M. A. TAYLOR

Earth Sciences Section
Leicestershire Museums, Arts
and Records Service
96 New Walk
Leicester LE1 6TD

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APPENDIX

Check-list of the pre-Penarth Group Triassic fishes of the British Isles (all material examined by B.G.G). MMG = Mercia Mudstone Group, SSG = Sherwood Sandstone Group.

Palaeobates keuperinus (Murchison and Strickland, 1840)
Bromsgrove Sandstone Formation (SSG) of Bromsgrove. Arden Sandstone Member (MMG) of Callow Hill; Mousley End; Shrewley; Knowle; Rowington; Shelfield Square, WARWICKSHIRE; and Burghill; Ripple; Pendock, HEREFORD and WORCESTER. Dane Hills Sandstone Member (MMG) of Shoulder of Mutton Hill; Dane Hills; New Parks; Aylestone Road, LEICESTERSHIRE.

Gyrolepis albertii Agassiz, 1835
Bromsgrove Sandstone Formation (SSG) of Bromsgrove, HEREFORD and WORCESTER (WARMS material). Colwick Formation (MMG) of Colwick Wood, NOTTINGHAMSHIRE. Arden Sandstone Member (MMG) Leamington, WARWICKSHIRE (Owen 1842 pl. 46, fig. 15; see Walker 1969). Dane Hills Sandstone Member (MMG) of Aylestone Road (*G. quenstedti* of Browne 1893) and Spinney Hills (BMNH P.41626–9), LEICESTERSHIRE.

Dictyopyge catoptera (Agassiz, 1835)
Sherwood Sandstone Group of Dungannon, CO. TYRONE.

Dictyopyge superstes (Egerton, 1858)
Arden Sandstone Member (MMG) of Rowington, WARWICKSHIRE. This record is based on a partial body and is probably part of a dictyopygid as Woodward (*in* Swinnerton 1925) surmized. It shows no resemblances to *Woodthorpea* despite Swinnerton's (1925, p. 97) comments, and closely resembles *Dictyopyge socialis* (Berger) from the Upper Keuper of Colburg.

Dictyopyge sp. nov.
Colwick Formation (MMG) of Colwick Wood, NOTTINGHAMSHIRE. Known from a single specimen (BMNH P.5288), this novel dictyopygid has scales with posterior margins bearing three prominent projections.

?*Perleidus*
Wildmoor Sandstone Formation (SSG), Aggborough, HEREFORD and WORCESTER. This record (White 1950) is based on a single specimen which lacks head and tail, but nevertheless closely resembles *Perleidus*.

Dipteronotus cyphus Egerton, 1854
Bromsgrove Sandstone Formation (SSG) of Bromsgrove, HEREFORD and WORCESTER and Otter Sandstone of Sidmouth, DEVON.

'*Semionotus*' *brodiei* Newton, 1887
Arden Sandstone Member (MMG) of Shrewley, WARWICKSHIRE. This species is represented by five syntypes (BMNH P.7615), which bear no resemblance to the genus *Semionotus* (McCune 1986, p. 229). It is a small species with large dorsal ridge scales and deep flank scales. The tail is heterocercal, the suspensorium more or less upright and supraorbitals seem to be present. It appears to be a catopterid or a redfieldiid.

Semionotus metcalfei Swinnerton, 1928
Colwick Formation (MMG) of Woodthorpe and Colwick Wood (BMNH P. 9818), NOTTINGHAMSHIRE. Dane Hills Sandstone Member (MMG) of Spinney Hills, LEICESTERSHIRE ('semionotid fish' of Horwood 1907). This species is probably synonymous with *S. kapffi* Fraas, 1861 (McCune 1986, p. 230). It has ridge scales with spines and a single large suborbital.

Woodthorpea wilsoni Swinnerton, 1925
Colwick Formation (MMG) of Woodthorpe, NOTTINGHAMSHIRE. This is a small semionotid, apparently with a single suborbital.

Ceratodus laevissimus Miall, 1878
Bromsgrove Sandstone Formation (SSG) of Coten End, WARWICKSHIRE (*Ceratodus* cf. *C. kurii* of Wills 1910) and Bromsgrove, HEREFORD and WORCESTER. Mercia Mudstone Group of Ripple, HEREFORD and WORCESTER.